THE FAMILIES AND GENERA OF THE LAMPRIDIFORM (ALLOTRIOGNATH) SUBORDER TRACHIPTEROIDEI[1]

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Owing to their scarcity, unusual shape, vivid coloration and frequently large size these fishes prompt discussion when captured or when occasional stranded individuals are found. In folklore some are associated with the abundance or scarcity of other species; thus the common names King-of-the-herring for *Regalecus glesne* among northern Europeans, and King-of-the-salmon for *Trachipterus trachypterus altivelis (= T. rex-salmonorum)* among Pacific Northwest Indians. *Regalecus glesne*, due to the fancied resemblance of its head and dorsal fin to a horse with fiery mane, when coupled with its immense size (estimated to 37 feet or more) and serpentine shape, may well be the basis for some of the reported sightings of sea serpents.

Three families, crestfishes, ribbonfishes and oarfishes, comprise the lampridiform suborder Trachipteroidei: Lophotidae, Trachipteridae, Regalecidae.[2] In recent years a comparatively large number of individuals belonging to this suborder, ranging in size from eggs to adults, has been taken on the shores and in the waters off the Americas. This material, together with specimens already in collections and the knowledge that has accumulated in the literature, offers opportunity to evaluate the systematics of the Trachipteroidei. Diagnoses for the suborder, families and genera are presented herein. In a subsequent paper the species will be enumerated, and the biology and evolution of the group will be discussed.

Representatives of all of the genera have been seen except for *Protolophotus* and *Agrostichthys*. The former is known from only two specimens found in Oligocene deposits of Iran (Arambourg, 1944; Walters, 1957). We are most grateful to G. M. Moreland, who examined two specimens of *Agrostichthys parkeri* in the Dominion Museum, Wellington, N. Z.; his observations form a large part of the generic diagnosis. All of the forms known from the Americas, including at least four un-

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[2] Members of all three families have been captured fairly frequently in California waters. At least five different species have been found in the stomachs of albacore and other deep-feeding tunas. However, before their role as potential competitors to, and food for, tunas (and other commercial species) can be determined, it is necessary to establish the characteristics of the group and to define the constituent parts (genera). This paper sets the stage for fishery workers to study these fishes not only in California but throughout the world.

described species, have been seen; all stages from egg to adult in *Zu* and *Trachipterus* are represented, all stages from larva to adult are represented for *Lophotus, Desmodema* and *Regalecus,* and *Eumecichthys* is represented only by subadults and adults. The number of specimens studied ranges from 5 of *Regalecus* to more than 100 of *Trachipterus.*

The material has been subjected to various methods of study: 1) external morphology and color pattern; 2) osteology through radiography, clearing and staining with alizarin, temporary clearing in glycerin, and dissection; 3) soft anatomy through dissection and histological work; 4) biometrics. Carl L. Hubbs generously turned over his notes and some radiographs on some of the anatomical features of California *Lophotus.* Norman B. Marshall kindly sent a radiograph of the type of *Eumecichthys fiski* which is in the British Museum (Natural History).

The anatomical studies on *Trachipterus arcticus* by Meek (1890), *Regalecus argenteus* by Parker (1886) and *Agrostichthys parkeri* by Dunbar (Benham and Dunbar, 1906) have been utilized, as well as a number of lesser papers which shall be cited when the species of trachipteroids are discussed. Through the perseverance of Italian students the egg development and morphology of the larvae have been made known for *Lophotus lacepedei* (Sanzo, 1940), *Zu cristatus* (Sanzo, 1918), *Trachipterus trachypterus* (LoBianco, 1908; Jacino, 1909) and *Regalecus glesne* (Sanzo, 1925); the information on *Trachipterus, Zu* and *Regalecus* was brought together by Spartà (1932).

Two studies on the metamorphosis of trachipterids were based on a mixture of species and thereby indicated a more profound series of morphological changes during ontogeny than actually occur; Emery's (1879 a, b) classical study on the metamorphosis of *Trachipterus t. trachypterus* (= *T. taenia*) employed larval flounders (*Arnoglossus* = *Ammopleurops,* see LoBianco, 1908) and Hubbs' (1926) study of *T. t. altivelis* (= *T. rex-salmonorum*) utilized a larval *Lophotus* sp. (specimen reexamined by Walters) for the small stages.

Many of the characters mentioned below refer to structures which are observable in few specimens because most trachipteroids become seriously damaged before they are finally preserved and put into a collection, and some of the characters apply to specific growth stages. A key designed to facilitate the identification of trachipteroids to genus is given at the end of the paper. Those differentiae were selected which should be determinable in all but the most badly damaged juveniles and adults, but the differentiae are not necessarily those we regard as the most significant for systematic purposes.

Order Lampridiformes (= Allotriognathi)

The group was established by Regan (1907) as a suborder of the Teleostei, and was later raised to ordinal status by him (1924). The outstanding feature is that the maxillae are protractile, they meet beneath the ascending processes of the premaxillae, and do not articulate with the palatines. For further details refer to Regan's papers. Regan (1907) stated the premaxillae of *Eumecichthys* are non-protractile but a radiograph of his specimen (the type of *Lophotes fiski*) shows them to be fully protracted.

Suborder Trachipteroidei (= Taeniosomi of Regan, and Trachipteroidei + Veliferoidei *ex parte* of Berg, 1940)

The frontals do not meet. A groove lies between the frontals, its floor containing the mesethmoid and orbitosphenoid ossifications; it receives the ascending processes of the maxillae and premaxillae when the jaw is retracted. The epiotics meet. The suborbital series is absent except for the lachrymal and jugal. The pelvic bones do not articulate with the coracoids. The pectoral fin-rays are inserted on the scapula and three radials; one radial contacts the scapula and two contact the coracoid. Some rays may be branched in the pectoral, pelvic and anal fins but the rays are otherwise simple; no rays are articulated except for the portion of the pelvic ray buried in the blade of the "oar" in *Regalecus* and the tip of the first dorsal ray in large adult *Eumecichthys*. Each dorsal fin-ray bears a spine on either side, at its base. In juveniles and young adults each fin-ray bears a series of spinelets, imparting a sandpapery texture. The anal fin is reduced in size or absent. The swimbladder when present does not extend past the anus. The vertebrae number 62-200. There are 6 or 7 branchiostegal rays and 0 to 10 pelvic fin-rays. The embryo passes through a tubular-eyed stage but free-living individuals have normal eyes.

Three families: Lophotidae, Trachipteridae, Regalecidae

Family Lophotidae

Unicornfishes, Crestfishes

The vertebrae in the rear of the body are of the same length as those in the beginning of the body. Ribs are present. The haemal spines following the anal fin are expanded to resemble hockey sticks. Branched but not articulated rays are present in the pectoral and sometimes also in the pelvic and anal fins. The anal fin is reduced in size. The anus is near the posterior end of the body and lies within a cloaca. An ink sac is present; this discharges into the cloaca. A physoclistic swimbladder is present. The lateral line plates are smooth. The lateral line terminates at the base of the caudal fin, in the dorsal part of the tail. The dorsal fin originates anterior to the eye. The skin is smooth, without tubercles, and the dermis possesses closely-spaced black striations. The first dorsal ray and the lowest, next to the lowest, or third lowest caudal ray are robust and quill-like. The head and body are covered with small deciduous imbricate cycloid scales. A basisphenoid and posterior myodome are present. The egg capsule is spiny and the larva hatches with two pelvic fin-rays.

Three genera: † *Protolophotus, Lophotus* and *Eumecichthys*

† *Protolophotus* Walters (1957)

GENOTYPE: *Lophotes Elami* Arambourg (1944)

The pelvic fins are well-developed and inserted on the mid ventral line. The pelvic bones end posterior to the posteleithra, and the pelvic fins have 6 rays. Vertebrae 79.

Lophotus Giorna (1809)

GENOTYPE: *Lophotus lacepede* Giorna (1809)

Maximum body depth is contained 5 to 8 times in standard length. The pelvic fins are small and inserted on the sides of the body, immediately below and behind the pectoral fins, and have 5 or 6 rays of which some may be branched. The pelvic bones lie parallel to the postcleithra. The anal fin base is longer than the pectoral fin base; there are 12 to 19 anal fin rays of which the posterior ones are branched. There are 220-263 dorsal fin-rays and 124-152 vertebrae. The swimbladder is well-developed and physoclistie; it consists of 3 chambers as follows: a thick-walled anterior chamber bearing the gas glands and receiving the retial supply anteriorly, above the esophagus; and two very long thin-walled posterior chambers which flank the ink sac. The ink sac begins beneath the latter half of the anterior chamber of the swimbladder. The color pattern is plain or spotted but never banded.

Eumecichthys Regan (1907)

GENOTYPE: *Lophotes fiski* Günther (1890)

Maximum body depth is contained 18.8 to 30 or more times in standard length. The pelvic fins, when present, are minute and inserted on the sides of the body immediately below and behind the pectoral fins, and have 2 or 3 rays of which 1 may be branched. The pelvic bones when present lie parallel to the postcleithra. The anal fin base is shorter than the pectoral fin base; there are 5 to 9 anal rays, none branched. There are 310-392 dorsal fin-rays and 151-200 vertebrae. The swimbladder is reduced in size; it consists of a single thick-walled anterior chamber. The ink sac begins approximately one head-length (*sans* rostrum) behind the rear of the swimbladder. The color pattern consists of numerous (24 to 60) dark subvertical bands.

Family Trachipteridae
Dealfishes

The vertebrae in the rear of the body are 2.5 to 4 times longer than those in the beginning of the body, in adults. Ribs are absent. The haemal spines are all of the same form, not resembling hockey sticks. The anal fin is absent. The anus is in the forward half of the body or slightly behind mid-body, and there is no cloaca. There is no ink sac. The swimbladder is rudimentary or absent. The lateral line plates bear spines. The lateral line terminates at the base of the caudal fin in the ventral part of the tail, or extends onto the ventral lobe of the caudal fin. The dorsal fin originates above or slightly behind the eye. The skin is fairly uniformly covered with osseous tubercles in the adult, not arranged in bands. The pelvic fins are inserted on the midventral line and the pelvic bones end posterior to the postcleithra. The basisphenoid and posterior myodome are present. The posttemporals cover the parietals. The egg capsule is smooth and the larva hatches out with 3 pelvic fin-rays. The rays in the nuchal pennant, pelvic fins, and lower lobe of the caudal fin (when present) tend to fragment and disappear with age.

Three genera: *Zu, Trachipterus* and *Desmodema.*

Zu, new genus

GENOTYPE: *Trachypterus cristatus* Bonelli (1820)

Some of the rays in the nuchal pennant and pelvic fins bear serially-arranged structures which are black and bulbous in the larva but eventually each becomes a pale-colored membranous flap containing a bean-shaped black body at the junction with the fin ray; the same structures appear on the caudal filament but much later in life. The caudal fin contains well-developed rays in the upper lobe which are set at an angle to the caudal peduncle; the rays in the lower lobe often fragment as the fish grows but their bases persist as spines. The late larva and juvenile (some adults) have a caudal filament, consisting of 1 or 2 rays in the ventral lobe which become very long and thread-like. The body is covered with cycloid, imbricated, deciduous scales. The tubercles along the midventral line are flattened. The ventral profile is scalloped between the pelvic fin bases and the beginning of the tail. The lateral line is straight on the trunk, wavy on the tail, and extends onto the caudal filament between the rays where it is once more straight. A physoclistic swimbladder is present in the larva and small juvenile; in subdults and adults it is a small white fibrous rudiment. The gastric caecum is short, extending less than half the distance from the pyloric valve to the anus in adults. There are about 1.5 pairs of lateral line plates per postanal vertebra. The anus is in the midventral line, before the middle and behind the anterior third of the body. The larva on hatching lacks rays in the "second dorsal fin"; only the rays of the nuchal pennant are present, and the first lies above the rear edge of the opercle. The early larva has two longitudinal rows of 4 black spots each; in the upper row, the first lies beneath the base of the nuchal pennant, the second midway between the first and the third, the third above the anus, and the fourth is before the middle of the tail; in the lower row, the first is above and behind the pectoral base, the second is above the anus, the third is on the tail below and behind the fourth spot on the upper series, and the fourth is at the base of the caudal fin. The juvenile and adult color pattern consists of about 6 wavy dark vertical bars on the dorsal part of the trunk and 4 on the ventral part; the tail has about 6 complete vertical dark bands which are narrower than the interspaces. There are 62-69 vertebrae, 3 to 7 pelvic rays and the caudal fin has 8-12 rays in the upper lobe with 1-5 in the lower.

Zu was the storm god of Babylonian mythology and is a fitting name to be applied to a trachipteroid since, until recent years, these fishes were known mainly from individuals found cast ashore in the wakes of storms.

Trachipterus Goüan (1770)

GENOTYPE: *Cepola trachyptera* Gmelin (1789)

The dorsal and pelvic fin-rays do not develop serially-arranged bulbous or flap-like structures. The caudal fin has well-developed rays in its upper lobe which are set at an angle to the caudal peduncle; the rays in the lower lobe fragment as the fish grows but their bases usually persist as spines. The late larva and juvenile have a caudal filament in which the second and third rays from the bottom of the lower lobe

become very long and thread-like; the longer (third) ray may develop serially-arranged black bulbous structures. Scales are absent. The tubercles are enlarged and sharp-tipped along the midventral line. The ventral profile is entire between the pelvic fin bases and the beginning of the tail. There is no trace of a swimbladder. The gastric caecum is short, ending closer to the pyloric valve than to the anus in adults. There is very nearly 1 pair of lateral line plates per postanal vertebra. The lateral line is straight on the tail, and terminates at the base of the caudal fin. The anus is on the midventral line and lies close to the midlength of the body in the adult. The larva hatches from the egg with rays developed in the anterior half of its dorsal fin, and the first dorsal ray is located above the eye. The newly-hatched larva has a dorsolateral and a ventrolateral streak of melanophores on its trunk. The juvenile has one or two horizontal rows of spots, each about equal to the eye in size, 1 to 5 spots per row; the spots in the ventral row tend to become longitudinal dark streaks; the dark markings tend to disappear in the adult. There are 69-101 vertebrae, 3 to 9 rays in each pelvic fin and the caudal fin has 6-10 rays in the upper lobe and 2-7 in the lower lobe.

Desmodema, new genus

GENOTYPE: *Trachypterus jacksoniensis polystictus* Ogilby (1897)

The dorsal, pelvic and caudal fin-rays do not develop bulbous or flap-like structures. The caudal fin rays are on the same axis as the caudal peduncle; a ventral lobe of the caudal fin is never present, and there is no caudal filament during ontogeny. The body is covered with non-imbricate, elliptical scales each with two slightly divergent spinose ridges (modified ctenoid). The tubercles along the midventral line do not develop sharp tips. The ventral profile is entire between the pelvic fin bases and the beginning of the tail. The lateral line is straight on the tail, and terminates at the base of the caudal fin. There is no swimbladder. The gastric caecum is long, ending closer to the anus than to the pyloric valve in the adult. There are more than two pairs of lateral line plates per postanal vertebra. The anus is often situated on the left or right side instead of on the midline; in a 365 mm. juvenile it lies in the forward third of the body, and is presumed to lie even further forward in intact adults. The egg and early larva are unknown. Over a size range of 11 to 365 mm. the head and trunk are covered with a large number of dark polka-dots. In adults polka-dots are absent. There are 104-109 vertebrae, 7 to 10 rays in each pelvic fin and the caudal fin has 5 to 8 rays.

Desmodema means "band body"; the name would be more correctly spelled "*Desmodemas*" but for euphony the terminal letter is deleted.

Family Regalecidae
Oarfishes

The vertebrae in the rear of the body are 1.5 to 5 times longer than those in the beginning of the body. Haemal spines are absent. The anal fin is absent. The anus is in the forward third of the body and there is no cloaca. There is no ink sac. The swimbladder is absent. The lateral line plates are smooth. The pelvic fins are inserted on the midventral line. The basisphenoid and myodome are absent. The posttemporals attach to the skull behind the parietals. The egg capsule is smooth and the larva hatches out with 3 pelvic rays.

Two genera: *Regalecus* and *Agrostichthys*.

The oarfishes have been considered by some authors to belong to two distinct families, Regalecidae and Agrostichthyidae while others combine the oarfishes and ribbonfishes into the single family Trachipteridae. The familial difference between the Lophotidae and Trachipteridae is unquestionable, to consider only the unique ink sac of the Lophotidae. And yet, the larva of *Zu cristatus* is so strikingly similar to the larva of *Lophotus lacepedei* that as a first impulse one might be tempted to regard *Zu* and *Lophotus* as congeneric. On the other hand, the larva of *Regalecus* differs strongly from those of *Lophotus*, *Zu* and *Trachipterus;* this, coupled with the osteological features listed above in addition to unique structural features possessed by *Regalecus* serves to separate further the oarfishes from the ribbonfishes. The structure of *Agrostichthys* is too imperfectly known to permit a more exhaustive family diagnosis at this time, and possibly it is at least subfamilially distinct from *Regalecus*.

Regalecus Brünnich (1771)

GENOTYPE: *Ophidium glesne* Ascanius (1788)

The dorsal fin begins above or before the anterior quarter of the orbit. Some of the rays in the nuchal pennant and pelvic fins have serially-arranged structures which are black and bulbous in the larva but in the juvenile (180 mm.) each becomes a pale-colored flap containing a black bean-shaped body at the junction with the fin ray; the same structures appear on the caudal fin of older juveniles; in subadults (1760+ mm.) these are pale-colored and glandular in appearance; in the adult these are represented by club-like fleshy thickenings and the blade of the pelvic "oar". The caudal fin rays are on the same axis as the caudal peduncle; there is no separate, ventral lobe of the caudal fin and there is no caudal filament formed. Scales are absent. The skin along the sides of the body is underlain by cartilage or white fibrous connective tissue, which is thickened to form 4 to 6 longitudinal ridges or carinae; a horizontal septum of cartilage or white fibrous connective tissue extends mediad from each carina to divide the muscle mass dorsad of the coelom into 5 pairs of cartilage or connective-tissue enclosed longitudinal compartments. These longitudinal structures completely disrupt the myotome pattern. The rounded tubercles are enlarged on the carinae, and the tubercles are widely separated between the carinae; along the midventral line the tubercles are verrucose. The ventral profile is entire. The lateral line is straight, runs above the lower quarter of the trunk on the next to the lowest carina, and consists of a chain of oblong plates set loosely in the skin, each plate pierced by a tube. The gill rakers are numerous (40-58), long and spiny. The gastric caecum is extremely long, ending about halfway between the anus and the tip of the tail. The anus is on the midventral line, in the anterior third of the body. The newly-hatched larva has a few melanophores along the base of the dorsal fin fold and around the bases of the pectoral fins. The late larva (24 mm.) has two longitudinal stripes of melanophores. Juveniles (45.8 mm.) have incomplete diffuse vertical bands and spots on the trunk; or the trunk and tail are covered with polka-dots (375-1240 mm.). The adult has irregular

oblique dark streaks on the trunk and polka-dots on the tail. The premaxillae are perpendicular to the frontal profile, and the maxillae are horizontally ovate. There are no teeth in the mouth. A suberanial crest is present. The large parietals extend forward between the frontals. The preorbital length of the neurocranium equals half the orbital diameter. Ribs are present. The vertebrae bear neural spines and haemapophyses, but haemal arches do not form. There are 143-151 mymeres (in the larva), 1 to 5 pelvic fin rays and 3 or 4 caudal fin rays aranged as in *Desmodema*.

Agrostichthys Phillipps (1924)

GENOTYPE: *Regalecus parkeri* Benham (1904)

The dorsal fin begins above or behind the posterior quarter of the orbit. Some of the rays in the nuchal pennant have serially-arranged bulbous structures. Scales are absent. The sides of the body are without carinae; though the bony tubercles are in six ill-defined longitudinal bands on each side of the body they are not grouped into alternating strips of large and small tubercles. The tubercles are flattened along the midventral line. The ventral profile is entire. The lateral line is straight and runs close to the midventral line on the trunk. The lateral line plates are bound in epidermis to form a continuous tube; there are small pores above and below the tube. The anus is on the midventral line, in the anterior third of the body. There are few gill rakers (8-10), all smooth. The gastric caecum does not extend past the anus. The color pattern of the adult consists of numerous broad dark complete vertical bands at regular intervals on the trunk and tail. The premaxillae extend forward in an almost straight line from the frontal profile, and the maxillae are vertically ovate. Teeth are present on the vomer and dentaries. There is no suberanial crest. The small parietals lie entirely behind the frontals. The preorbital length of the neurocranium is about equal to the diameter of the orbit. The vertebrae throughout are represented only by scarcely osified centra; there are no spines or other processes. There are an estimated 170 vertebrae, and 1 pelvic fin ray; the caudal fin is unknown.

ARTIFICIAL KEY TO THE FAMILIES AND GENERA OF THE TRACHIPTEROIDEI

1a. Anus near posterior end of body. Anal fin present. Skin smooth. Ink sac present in recent forms. LOPHOTIDAE (2)

1b. Anus near middle of body, or further forward. Anal fin absent. Skin roughened by numerous bony tubercles. Ink sac absent. (4)

2a. Pelvic fins inserted on midventral line. Vertebrae 79. Oligocene. † *Protolophotus*

2b. Pelvic fins absent or inserted on sides of body, close to pectoral fins. Vertebrae more than 120. Recent.

3a. Body depth 5 to 8 in standard length. Anal fin base longer than pectoral fin base. Color pattern plain or spotted. Vertebrae 124-152. *Lophotous*

3b. Body depth 18.8 to 30 in standard length. Anal fin base much shorter than pectoral fin base. Color pattern banded. Vertebrae 151-200. *Eumecichthys*

4a. Basisphenoid and posterior myodome present. Lateral line plates each with a spine. Bony tubercles not arranged in ill-or well-defined lengthwise bands along the sides of the body. Vertebrae 62-109. TRACHIPTERIDAE (5)

4b. Basisphenoid and posterior myodome absent. Lateral line plates smooth. Bony tubercles arranged in ill-defined lengthwise bands or pronounced lengthwise ridges, along the sides of the body. Vertebrae 143 to about 170. REGALECIDAE (7)

5a. Ventral profile scalloped between pelvic fin bases and beginning of tail. Lateral line wavy on tail. Tubercles flattened on midventral line. Color pattern of dark vertical bars or bands. Deciduous imbricated cycloid scales. Vertebrae 62-69. *Zu*, new genus.

5b. Ventral profile entire. Lateral line straight on tail. Color pattern uniform, polka-dotted, or with few large dark spots or longitudinal streaks. Tubercles flattened or sharp-tipped. Scales absent or ctenoid. Vertebrae 69-109. (6)

6a. Color pattern uniform or with several equidistant eye-sized black spots and usually one or more longitudinal dark streaks. Tubercles along midventral line sharp-tipped. Scales absent. One pair of lateral line plates per postanal vertebrae. In adults, tip of gastric caecum lies nearer pyloric valve than anus. Caudal fin with 6 to 10 rays in the upper lobe, which is set at an agle to the caudal peduncle, and 2 to 7 rays or their rudiments in the lower lobe. Vertebrae 69-101. *Trachipterus.*

6b. Color pattern uniform or polka-dotted. Tubercles along midventral line are not sharp-tipped. Deciduous nonoverlapping modified ctenoid scales. Two or more pairs of lateral line plates per postanal vertebrae. In adults, tip of gastric caecum lies closer to anus than to pyloric valve. Caudal fin of 5 to 8 weak rays parallel with caudal peduncle. Vertebrae 104-109. *Desmodema*, new genus.

7a. Gill rakers 40-58. Premaxilla set at right angle to frontal profile, maxilla horizontally ovate. Gastric caecum extends well past anus. Color pattern of irregular oblique stripes and polka-dots. *Regalecus.*

7b. Gill rakers 8-10. Premaxilla continues forward in line with frontal profile, maxilla vertically ovate. Gastric caecum ends before anus. Color pattern banded. *Agrostichthys.*

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